

A CHEMOTAXONOMIC CLASSIFICATION OF THE SOLANACEAE¹

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ABSTRACT

Alkaloids and steroids in the Solanaceae are reported extensively in the literature. By examining the biosynthetic routes leading to different alkaloids, the pathways can be visualized as a spiral from which the various compounds can be derived. Arrangement of the genera of Solanaceae according to their chemical contents in relationship to this spiral supports traditional classifications of the family, but the Anthocercidoideae and Atropoideae must be recognized as new subfamilies due to their biochemical synthesis syndromes. Similarly, Solaninae and Physalinae must be accepted as separate subtribes of tribe Solaneae because of their differing and exclusive steroid synthesis. *Acnistus* and *Dunalia* must be allied with *Jaborosa* in tribe Jaboroseae.

Although solanaceous species are well known to afford an array of alkaloids and steroids, the family has not been arranged yet according to chemical features. Indeed, it is difficult to find reports of most features because, except for the occurrence of calcium oxalate crystals, only their absence is recorded. Thus Philipson (1977) concluded that a lack of iridioids characterizes the Solanaceae within the Unitegminae. Dahlgren (1975, 1980) came to similar conclusions, adding the deficiency of polyacetylenes as a characteristic. Sporne (1980) believed that absence of leucoanthocyanins and ellagitannins are chemical characteristics of the family and indicated that whether or not the seeds contain endosperm may or may not be significant.

In an investigation of the cytochrome-C and plastocyanin amino acid sequence, Boulter et al. (1979) placed the Solanaceae far from the Asteraceae in their family tree, and although they related it closely to the Scrophulariaceae, they surprisingly considered the Caprifoliaceae to be the most closely related family. This biochemical statement supports the earlier view of Chadeffaud & Emberger (1960) that the Solanaceae and Caprifoliaceae are closely related based on embryological characters. Nevertheless, mature solanaceous plants are typical alkaloid-accumulators, whereas mature caprifoliaceous plants have phenol-glycosides (Hegnauer, 1973). In the same publication Boulter et al. (1979) put the tomato alongside the potato and separated tobacco and the woody *Solanum crispum* Ruiz & Pavón, and they held *Capsicum frutescens* L. to be signifi-

cantly different from the preceding species based on the amino acid complement.

The use of active principles found in different Solanaceae to construct systematic schemes can be accepted only when it can be demonstrated that the biosynthetic routes leading to these chemical structures are homologous (Tétényi, 1973). The valid chemical patterns are in the various biosynthetic pathways and not in the substances accumulated. Thus I have summarized the branching and relationships of biosynthetic pathways in alkaloid production in the Solanaceae in Table 1 and Figure 1. Numbers in the following paragraphs correspond to those of Table 1 and Figure 1.

The first evidence supporting this scheme lies in the well-known, genetically determined chemical differentiation in infraspecific chemotaxa of *Duboisia myoporoides* R. Br. (Tétényi, 1970). The characteristic active alkaloid ingredient, nicotine (1), in one chemotaxon of this species is the result of the synthesis of ornithine and tryptophan to an alkaloid. Another chemotaxon of *D. myoporoides* is characterized by a splicing of the aspartate pattern (lysine) and acetyl-CoA to the alkaloid biosynthesis, and the main alkaloids are then anabasine (A) and isopelletierine (B). In a third infraspecific chemotaxon, an entirely different pattern occurs: an α -face nucleophilic attack instead of the β -face one of the N-methyl- Δ^1 -pyrrolinium salt (Fig. 2; Leete, 1979) leads to the pathways indicated by the solalkoid spiral (Fig. 1), that is, the linking of ornithine and acetyl-CoA to hygrine (2) and then the development

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TABLE 1. Alkaloids of Solanaceae included in and arranged conforming to the solalkoid spiral.

Nicotine and its derivatives		
nicotine (1) C ₁₀ H ₁₄ N ₂ [54-11-5]	anabasine (A) C ₁₀ H ₁₄ N ₂ [494-52-0]	isopelletierine (B) C ₈ H ₁₅ NO [539-00-4]
Tropane alkaloids		
hygrine (2) C ₈ H ₁₂ N ₂ O ₃ [496-49-1]	hygroline (2) C ₈ H ₁₇ NO [1617-83-0]	withasomnine (3) C ₁₂ H ₁₅ N ₂ [10183-74-1]
	cuscohygrine (4) C ₁₃ H ₂₄ NO ₄ [454-14-8]	belladonnine (4) C ₃₄ H ₄₂ N ₂ O ₄ [6696-63-5]
tropinone (5) C ₈ H ₁₃ NO [532-24-1]	physoperuvine (5) C ₈ H ₁₅ NO [60723-27-5]	tropine (5) C ₈ H ₁₅ NO [120-29-6]
	isovaleryloxytropane (6) C ₁₃ H ₂₃ NO ₂ [490-96-0]	seneciolyoxytropane (6) C ₁₃ H ₂₁ NO ₃ [77101-57-6]
tigloidine (7) C ₁₃ H ₂₁ NO ₂ [495-83-0]	tigloyoxytropane (7) C ₁₃ H ₂₁ NO ₃ [55727-41-8]	valtropine (7) C ₁₃ H ₂₃ NO ₂ [495-82-9]
scopolamine (8) C ₁₃ H ₂₁ NO ₄ [51-34-3]	hyoscyamine (8) C ₁₇ H ₂₁ NO ₃ [101-31-5]	physochlaine (8) C ₁₇ H ₂₃ NO ₃ [54357-41-4]
Other alkaloids		
fabianine (—) C ₁₄ H ₂₁ NO [6871-51-8]	β-carboline (C) C ₁₅ H ₂₁ N ₂ O ₃ [244-63-3]	capsaicine (D) C ₁₈ H ₂₇ NO ₃ [54357-41-4]
	betaine (E) C ₁₅ H ₁₁ NO ₂ [107-43-7]	choline (E) C ₅ H ₁₅ NO ₂ [62-49-7]

Explanation: common name; symbols in parentheses refer to Figure 1

formula
[registry number]

of other simple and ester tropane alkaloids. Thus pyruvate-leucine yields valeroidine (6) with iso-valeric acid; aspartate-isoleucine yields tigloidine (7) with tiglic acid; and finally, from phenylalanine and tropic acid, scopolamine (8) becomes the characteristic alkaloid of the third chemotaxon.

The genus *Duboisia* R. Br. provides further evidence of this kind of chemical differentiation separating the infraspecific taxa of *D. myoporoides* from one another. In *D. hopwoodii* F. Muell., nicotine (1) and its derivatives are synthesized by the β-face attack of ornithine, whereas in *D. leichhardtii* F. Muell.—the most economical source in the world for scopolamine—this alkaloid is accumulated through the converse formation. Thus the scheme in Figure 1 is true for *Duboisia* as a genus as well as for its components.

Two other genera examined in subfamily Anthocercidoideae (described on p. 607)—which

includes *Duboisia*—show the same diversity in alkaloid biosynthesis, having a broad spectrum of alkaloids, and those from nicotine (1), anabasine (A), cuscohygrine (4), to tropine (5), valeroidine (6), tigloidine (7), and scopolamine (8) have been detected.

Alkaloid synthesis in subfamily Cestroideae Schldl. also proceeds according to Figure 1, but here the main stopping points are nicotine and its derivatives, a somewhat different picture from the Anthocercidoideae. Thus nicotine (1) is the sole product in the genus *Cestrum* L., whereas fabianine, a tetrahydroquinoline alkaloid arising from a biosynthesis preceding the pyridine-nucleotide cycle, is accumulated as well as nicotine in *Fabiana* Ruiz & Pavón. The aspartate-lysine path is switched in *Streptosolen* Miers, and anabasine is accumulated in addition to nicotine. The alkaloid spectrum of *Nicotiana* L. and *Salpiglossis* Ruiz & Pavón by intervention of acetyl-CoA, accumulates isopelletierine (B) in addition

SOLALKOID SPIRAL

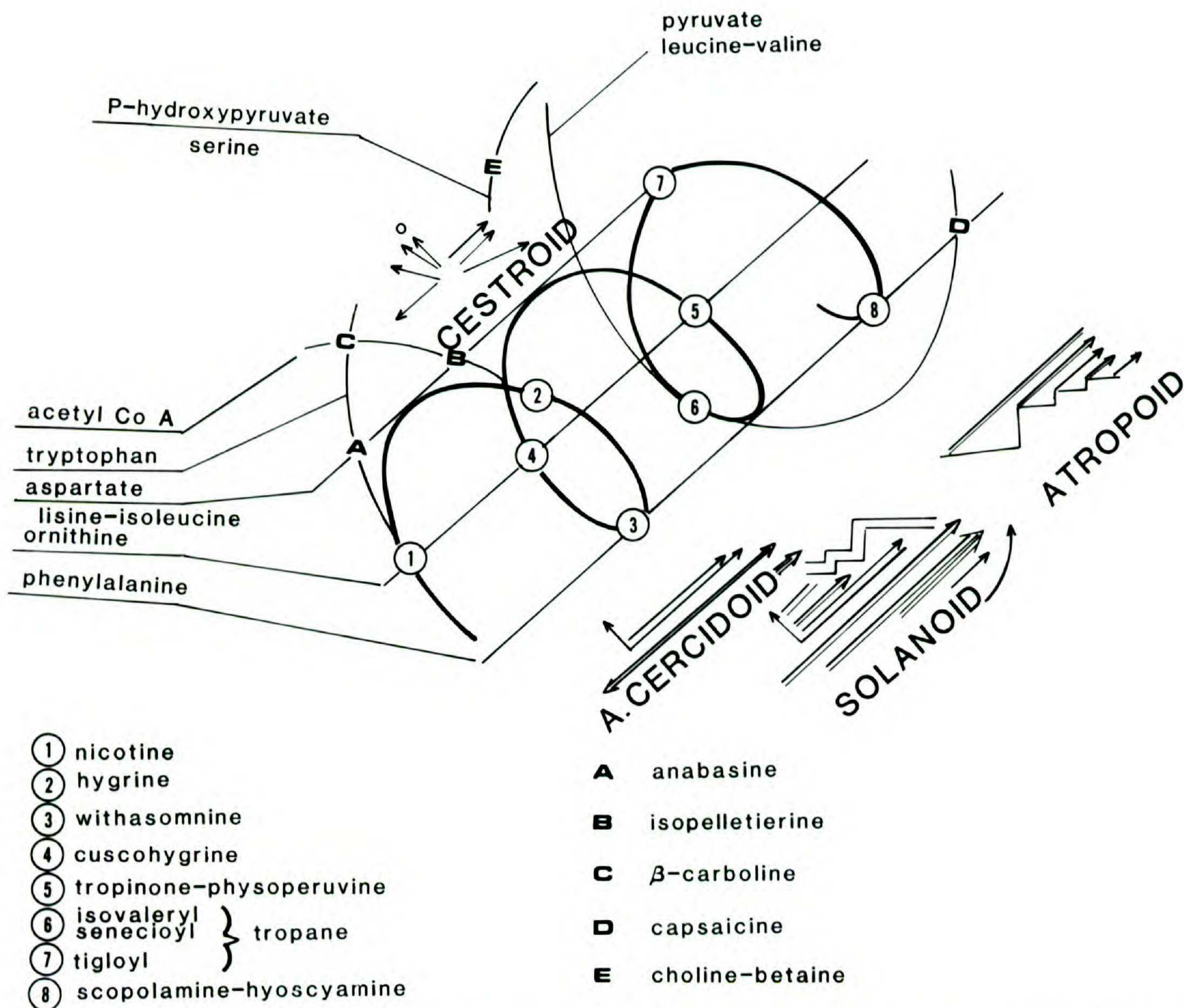


FIGURE 1. Solalkoid spiral based on characteristic biosynthetic patterns of most important alkaloids isolated from plants belonging to the Solanaceae. Amino acids represent starting and combined points. Patterns of alkaloid biosynthesis in subfamilies are clarified in the text.

to the above substances. *Nicotiana* is even enriched by betaine (E) through the hydroxypyruvate-serine pathway. Coupling of acetyl-CoA with tryptophan is the source of the simple indolalkaloid of *Vestia* Willd., which contains a β -carboline skeleton.

My scheme might not be tenable if the Cestroideae were not differentiated chemically also. In fact, the alkaloid biogenesis of hygrine derivatives is found in this subfamily too, although only *Brunfelsia* L. accumulates just cuscohygrine (4) and pyrrole-3-carboximidine, which was also detected in *Nierembergia* Ruiz & Pavón, whereas real tropane esters are synthesized in *Schizanthus*

Ruiz & Pavón. However, the alkaloid spectrum in *Schizanthus* is unique in the whole family with its hygroline (occurring also in the Erythroxyllaceae) and because the senecioyl and angeloyl tropane esters (6) are formed from pyruvate-leucine and ornithine. Formation of the alkaloid valeroidine in *Schizanthus* by this biosynthetic pathway is characteristic of the family Solanaceae as well as of *Anthocercis* Labill., *Cyphanthera* Miers, and *Duboisia*. However, taking into account the two kinds of hygrine synthesis, the predominance of nicotine in its various derivatives (A, B, C), and the primary substances brunfelsamine and fabianine, we can assert that the

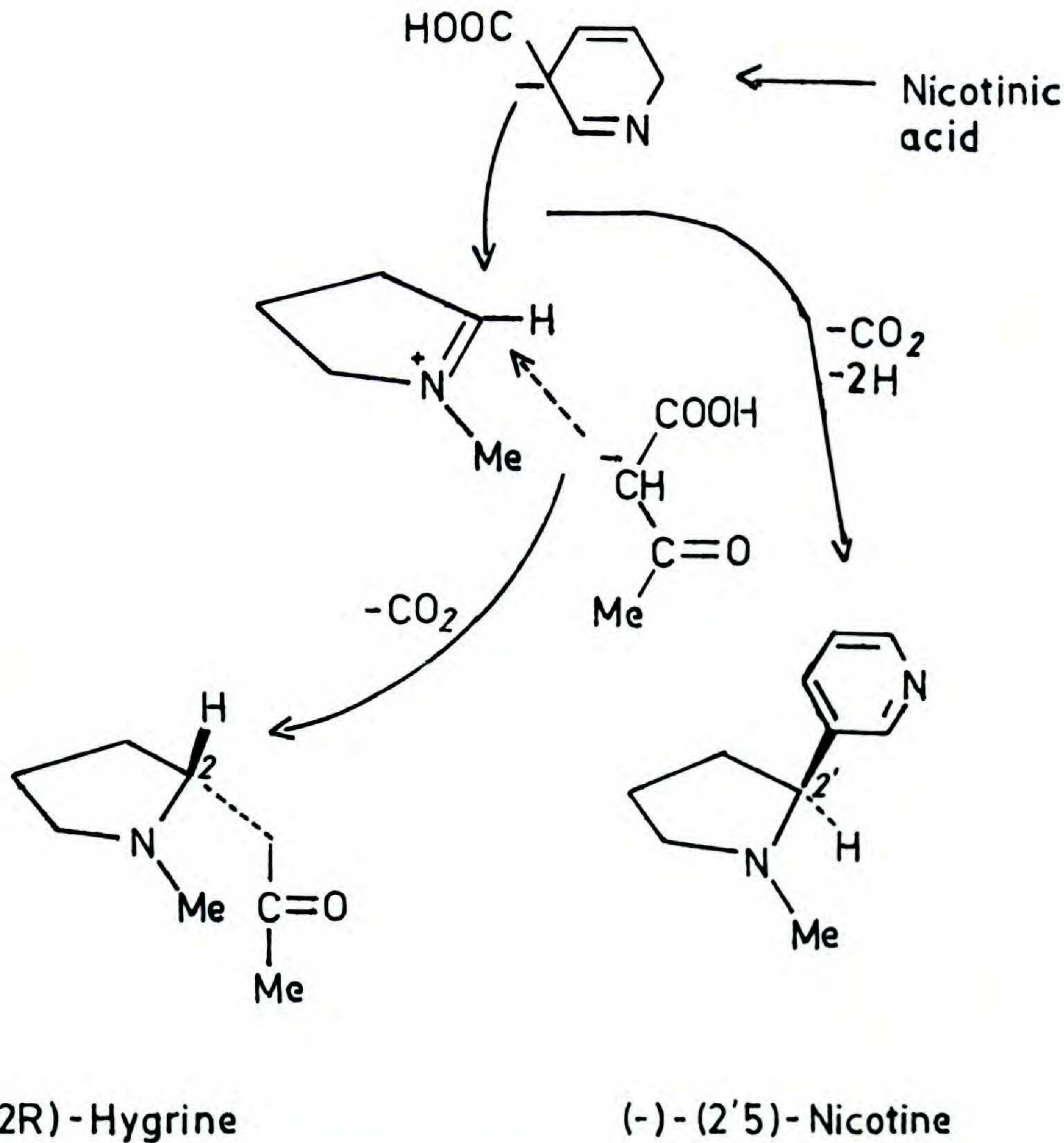


FIGURE 2. Nucleophilic attack of N-methyl- Δ^1 -pyrrolinium salt from the α - and β -face (Leete, 1979).

chemical differentiation of the Cestroideae, in having an alkaloid synthesis with several similarities to that of the Erythroxylaceae, Rubiaceae, Elaeagnaceae, and Malpighiaceae, significantly surpasses that of the Anthocercidoideae.

Chemical differentiation in subfamily Solanoideae is of a different character than in the Cestroideae, for here the hygrine derivatives are always preponderant, and the differences are in the ever-increasing complexity of the molecular entities synthesized by the different genera as if overcoming a barrier. Similar to the case of *Brunfelsia* mentioned above, the *Solanum* L., *Jaltomata* Schldl. (*Saracha viscosa* Schrader), and *Margaranthus* Schldl. arrested at a certain stage, accumulate cuscohygrine (4) only. *Nicandra* Adans. starts from hygrine (2) and, like *Cyphomandra* Sendtner, reaches the formation of tropinone (5). The alkaloid physoperuvine (5) of *Physalis* L. is equivalent to this, although tigloidine (7), an alkaloid of this genus, is an ester but not with tropic acid. In *Withania* Pauquy aspartate-isoleucine and ornithine are synthesized to 3'-tigloyloxytropine without the pres-

ence of any tropic ester, but the alkaloid spectrum of this genus is very broad; thus withasomnine (3) is formed by coupling ornithine to phenylalanine. Isopelletierine (B) from lysine and acetyl-CoA and even the alkaloid choline (E) arise from the hydroxypyruvate synthesis pathway. These are only the main types represented. In the genera *Leucophysalis* Rydb. (*Physaliastrum japonicum* (Franchet & Savat.) Honda) and *Lycium* L. of this subfamily, the unique alkaloid detected so far is betaine (E), formed from the serine cycle in the same way as choline.

Affinity of subfamily Solanoideae with subfamily Anthocercidoideae is proven in the alkaloid spectra of *Brugmansia* Pers. and *Datura* L. On the one hand, these plants realize both synthetic routes from nicotine (1) to scopolamine (8), while on the other hand, they also form and accumulate the alkaloid valeroidine (6) like *Anthocercis* and *Duboisia*. In the genus *Solandra* Sw., valtropine (7), originating from the coupling of isoleucine with ornithine, follows a path of alkaloid biosynthesis homologous to that in *Cyphanthera* and *Grammosolen* Haegi. However,

TABLE 2. Differences of N-methyl- Δ^1 -pyrrolinium derivative alkaloids in subfamily Atropoideae. Data from Romeike (1978) except where noted otherwise.

Alkaloids	Genus							
	<i>Atropa</i>	<i>Hyoscyamus</i>	<i>Scopolia</i>	<i>Whitleya</i>	<i>Mandragora</i>	<i>Przewalskia</i>	<i>Atropanthe</i>	<i>Physochlaina</i>
Physochlaine								+
Hyoscyamine	+	+	+	+	+	+	+	+
3'-tigloyloxytropene		+	+		+			
Belladonnine	+				+			
Tropine	+	+	+	+				
Tetramethylputrescine		+						
Δ -N-methylornithine (Hedges & Herbert, 1981)	+							

a related feature in the genus *Anthotroche* Endl. may be that hyoscyamine (8) predominates in the spectrum. The hygrine (2) of *Salpichroa* Miers also shows relationship to *Duboisia*, but here hyoscyamine (8) is the characteristic alkaloid, similar to the content of tigloidine (7) in *Acnistus* Schott and the small amount of scopolamine (8) in *Latua* Phil. The combination of pyruvate-valine and phenylalanine to capsaicine (D) supports the curious alkaloid biosynthesis and the isolation of *Capsicum* L. as stated by Boulter et al. (1979).

The system shown in Figure 1 is also supported by the alkaloid synthesis in subfamily Atropoideae (described on p. 607). In contrast to the Solanoideae, the simple alkaloid synthesis of the Atropoideae is subordinate to that of tropane esters. This is illustrated by the data in Table 2, for initially nicotine formation is only inhibited—as exemplified by *Atropa* L. and *Hyoscyamus* L.—and the genera *Scopolia* Jacq. and *Whitleya* Sweet (*Anisodus* Link) are the most advanced cases in which a simple tropane base could be detected. Occurrence of tigloyl ester (7) can be verified in *Mandragora* L. only by the presence of cuscohygrine (4) and a little scopolamine (8). *Przewalskia* Maxim. and *Atropanthe* Pascher accumulate mainly hyoscyamine (8), which is characteristic in the whole family and occurs in each genus. Although the result of the synthesis in *Physochlaina* G. Don is also predominantly hyoscyamine, its peculiar alkaloid, physochlaine (8), is the tropane ester of 4-methoxyphenylacetic acid, a phenylalanine derivative.

The alkaloid-forming distinctions of solanaceous taxa at various levels have been arranged according to Figure 1. The requirements were satisfied by this scheme, which we have termed the solalkoid spiral. One objection may be that I have not mentioned the connection between terpenoid and alkaloid biosynthesis. This is because the steroid synthesis that is characteristic of the family is exclusive, alternative, and without transition, in contrast to the process of alkaloid synthesis, which is gradual and proceeds by inhibition.

This is supported by the studies of infraspecific chemotaxa carried out with withanolides on *Withania somnifera* Dunal (Lavie, 1973) as well as our own analysis of steroidal alkaloid taxa of *Solanum dulcamara* L. (Tétényi et al., 1977). No instance of a steroidal alkaloid in a withanolide-containing species or the reverse is known, although this may be due to deficiency in our equipment or methods.

It seems that these two routes of steroid synthesis—steroidal alkaloids versus lactones—represent a phylogenetic branching alternative with cholesterol as its starting point. Oxidation leads to withanolides compared with partial etherification to neutral saponins, followed by cyclization to steroidal alkaloids.

Duboisia—subfamily Anthocercidoideae—synthesizes only neutral sapogenins, and *Cyphanthera*, *Anthotroche*, *Crenidium* Haegi ursoic acid only, a further feature pointing to their primordial endemism. Simple sapogenins were detected in subfamily Cestroideae: in *Combera* Sandw., *Fabiana*, *Nierembergia*, *Browallia* L.,

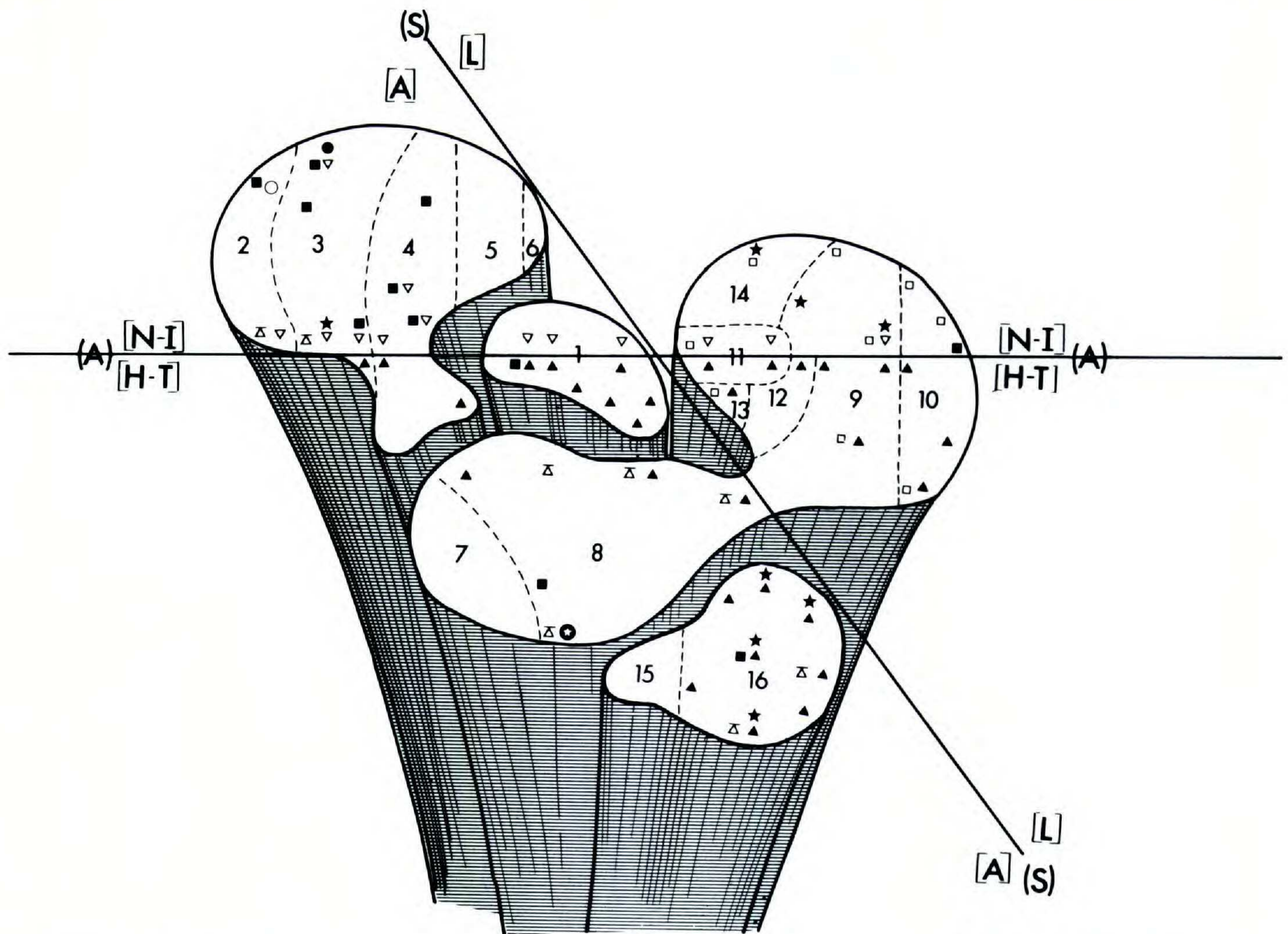


FIGURE 3. Chemotaxonomic system of the Solanaceae based on characteristic alkaloids and steroids of genera in four subfamilies containing 16 tribes and designed following Dahlgren (1975). Axes separate most important biosystematic systems. Steroid (S): ■ = sapogenin, ▴ = alkaloid [A], □ = lactone [L]. Alkaloids (A): ▽ = nicotine-isopelletierine type [N-I], ○ = β -carboline, ● = isoquinoline, ★ = choline-betaine, ▲ = hygrine-tropane type [H-T], ● = capsaicine. Anthoceroideae.—1. Anthoceraceae G. Don. (7). Cestroideae.—2. Cestreae G. Don. (5).—3. Nicotianeae G. Don. (8).—4. Salpigloss[id]eae Benth. (7).—5. Schwenckieae A. T. Hunz. (3).—6. Parabouchetieae A. T. Hunz. (1). Solanoideae.—7. Juannulloae A. T. Hunz. (8).—8. Solaneae–Solanineae (15).—9. Solaneae–Physalinae (9).—10. Jaboroseae Miers (7).—11. Datureae Reichb. (2).—12. Solandreae Miers (2).—13. Nicandreae Wettst. (1).—14. Lycieae A. T. Hunz. (3). Atropoideae.—15. Discopodiineae Baehni (2).—16. Atropeae Reichb. (9). Numbers in parentheses indicate numbers of genera.

Salpiglossis, *Vestia*, and *Streptosolen*, as well as in *Cestrum* and *Nicotiana*, but these two have steroidal alkaloids.

Subfamily Solanoideae, apart from *Exodeconus* Raf., shows a prevalence of steroidal alkaloids when the genera *Solanum*, *Cyphomandra*, *Capsicum*, and *Lycopersicon* Miller are considered. Because of their steroidal lactone synthesis, *Physalis*, *Withania*, *Witheringia* L'Hér., *Acnistatus*, *Datura*, *Nicandra*, and *Lycium*, as well as *Dunalia* Kunth and *Jaborosa* Juss. and the sapogenin-containing *Trechonaetes* Miers, should be evaluated as quite distinct. This differentiated steroid synthesis divides subfamily Solanoideae. The connection between alkaloid and steroid biosynthesis is shown by the fact that *Solanum*,

arrested at cuscohygrine, includes species accumulating steroidal alkaloids building in arginine released from the ornithine cycle in their genesis.

The genera *Physochlaina* and *Scopolia* of subfamily Atropoideae synthesize solanidine. *Hyoscyamus* synthesizes sapogenin, and thus the subfamily is nearer to the subtribe of the Solanoideae characterized by formation of the same steroids.

If we base a chemical classification of the Solanaceae on the facts mentioned above, we cannot accept the analysis of Evans (1979) or Romeike (1978), who considered only alkaloid properties in evaluating Wettstein's century-old system. I have developed in Figure 3 a chemotaxonomic classification of the Solanaceae. It

TABLE 3. Characteristic alkaloids and steroids for the chemotaxonomic system of the Solanaceae (corresponding to Fig. 3).

Tribe	Genus	Alkaloid	Steroid
1	<i>Anthocercis</i>	hyoscyamine, ¹⁰ scopolamine ¹³	†
	<i>Anthotroche</i>	hyoscyamine ¹⁰	
	<i>Crenidium</i>	hyoscyamine, ¹⁴ anabasine ¹⁴	†
	<i>Cyphanthera</i>	scopolamine, ¹⁴ nicotine ¹⁴	†
	<i>Duboisia</i>	scopolamine, ¹ isopelletierine ¹	sapogenin ³
	<i>Grammosolen</i>	scopolamine ¹⁰	
	<i>Symonanthus</i>	tigloyl esters ¹⁰	
2	<i>Cestrum</i>	nicotine ³	solasodin ³
	<i>Vestia</i>	β-carboline ¹⁷	diosgenin ³
3	<i>Combera</i>	—	sapogenin ³
	<i>Fabiana</i>	nicotine, fabianine ³	sapogenin ³
	<i>Nicotiana</i>	betaine, ⁷ isopelletierine ¹	solasodin ³
	<i>Nierembergia</i>	β-tigloyloxytropane + brunfelsamine ¹⁵	sapogenin ⁴
4	<i>Browallia</i>	—	sapogenin ³
	<i>Brunfelsia</i>	cuscohygrine ³ + brunfelsamine ¹⁶	—
	<i>Salpiglossis</i>	isopelletierine ¹	sapogenin ³
	<i>Schizanthus</i>	seneciolyoxytropane, ⁶ hygrolines ¹	—
	<i>Streptosolen</i>	anabasine ³	sapogenin ²
8	<i>Capsicum</i>	capsaicine ³	solanidin ²
	<i>Cyphomandra</i>	tropinone ¹	solasodin ¹
	<i>Exodeconus</i>	—	neotigogenin ³
	<i>Jaltomata</i>	cuscohygrine ⁵	—
	<i>Lycopersicon</i>	—	tomatin ⁷
	<i>Solanum</i>	cuscohygrine (solamine) ⁸	solasodin ³
9	<i>Leucophysalis</i>	betaine ³	—
	<i>Margaranthus</i>	cuscohygrine ⁸	—
	<i>Physalis</i>	tigloidine, ¹ physoperuvine ¹	physalin ³
	<i>Withania</i>	choline, isopelletierine, 3'-tigloyloxytropane ¹	withanolide ³
	<i>Witheringia</i>	—	physalin ⁹
10	<i>Acnistus</i>	hyoscyamine ¹⁰	withanolide ¹¹
	<i>Dunalia</i>	—	withanolide ¹¹
	<i>Jaborosa</i>	—	steroidlactone ¹¹
	<i>Latua</i>	hyoscyamine ¹	—
	<i>Salpichroa</i>	hyoscyamine ¹	—
	<i>Trechonaetes</i>	—	sapogenin ³
11	<i>Brugmansia</i>	nicotine, scopolamine ¹	—
	<i>Datura</i>	nicotine, scopolamine ¹	withanolide ³
12	<i>Solandra</i>	hyoscyamine ¹	—
13	<i>Nicandra</i>	tropinone ¹	withanolide ³
14	<i>Lycium</i>	betaine ³	withanolide ³
16	<i>Atropa</i>	choline, ¹² hyoscyamine ⁷	—
	<i>Atropanthe</i>	hyoscyamine ¹	—
	<i>Hyoscyamus</i>	choline, ¹² hyoscyamine ¹	sapogenin ³
	<i>Mandragora</i>	hyoscyamine ¹	—
	<i>Physochlaina</i>	physochlaine ¹	solanidin ³
	<i>Przewalskia</i>	hyoscyamine ¹	—
	<i>Scopolia</i>	choline, ¹² hyoscyamine ¹	solanidin ³
	<i>Whitleya</i>	choline, ¹² hyoscyamine ¹	—

† Ursolic acids present.¹⁴

¹ Romeike, 1978; ² Gibbs, 1974; ³ Hegnauer, 1973; ⁴ Lorenti et al., 1981; ⁵ Evans, 1979; ⁶ San Martin et al., 1980; ⁷ Paris & Moyse, 1971; ⁸ Evans & Somanabandhu, 1980; ⁹ Antoun et al., 1981; ¹⁰ Evans & Ramsey, 1981; ¹¹ D'Arcy, 1979; ¹² Gessner, 1977; ¹³ Evans & Ramsey, 1983; ¹⁴ El Imam & Evans, 1984; ¹⁵ Buschi & Pomilio, 1986; ¹⁶ Lloyd et al., 1985; ¹⁷ Faini et al., 1980.

considers the chemosyndrome of the Solanaceae, has reference to the cross-sectional presentation of Dahlgren (1975, 1980), and draws upon the systematic data of D'Arcy (1979), Haegi (1979, 1981), and Hunziker (1979).

The surface dimensions of the four subfamilies correspond to the number of included genera, while the curves involving the subfamilies label the affinity points of the homologous chemical qualities. The two main trends of alkaloid synthesis in the family—accumulation of nicotine-isopelletierine or hygrine-tropane type alkaloids—branch from the horizontal axis; the inclined axis separates the steroidal lactone and steroidal alkaloid taxa. Tribes of the subfamilies are shown by numbers and dotted lines. I have divided the tribe Solaneae Reichb. into subtribes Solaninae (Solanineae Dunal) and Physalinae (Physalidineae Reichb.) on the basis of different and exclusive types of steroid synthesis and considering the data of Baehni (1946) and others. *Acnistus* and *Dunalia* are placed in tribe Jaboroseae Miers in accordance with Baehni on the basis of their steroidal lactone content. *Latua* was similarly treated—its bent embryo agrees with this placement and its alkaloid chemistry precludes assigning it to subfamily Cestroideae.

The characteristic alkaloid or steroidal data for the genera shown in Figure 3 are also shown in Table 3. I have not found reliable recent data on the alkaloid or steroid active ingredient of four tribes and 43 genera; however, I feel justified in presenting this review, a novel chemotaxonomic evaluation of facts known to others, and a classification system for the Solanaceae.

This new system consists of four subfamilies. We must separate the Anthocercidoideae from the Cestroideae, and the Atropoideae from the Solanoideae because of differences in area of origin, morphology, flowers, and chemistry. The Anthocercidoideae have ancestral characteristics and are endemic to Australia. They differ morphologically from the Cestroideae by having long, narrow corolla lobes, finely striated corolla tubes, and distinctive sculptured pollen grains. Their chemosyndrome combines predominantly hygrine derivatives—characteristically scopolamine—with neutral sapogenins, while the Cestroideae have chiefly nicotine derivatives together with simple and complex steroidal alkaloids, and only one tropane ester alkaloid in common with the Anthocercidoideae.

The Atropoideae, which have a distinctive alkaloid-tropane ester synthesis relationship, differ

also in having dispersed from their ancestral center. They are adapted to withstand cold seasons in Eurasia and have become isolated on islands or high mountains in Africa. The Atropoideae differ morphologically from the Solanoideae by having imbricate corolla lobes, whereas Solanoideae have valvate—sometimes twofold valvate—aestivation. The Atropoideae chemosyndrome combines highly derived tropane ester alkaloids with steroidal alkaloids, while the Solanoideae possess one of these biosyntheses but have the other only in inhibited form as simple tropanes or as steroidal lactones. These evolutionary patterns are sufficient to warrant recognition of the taxa as subfamilies.

Subfamily ANTHOCERCIDOIDEAE Tétényi, subfam. nov.

Plantae frutescentes caulibus lignosis in Australia habitantes. Aestivatio valvato-aperta. Corolla regulariter quinquelobata. Lobi involuti, prope nervum medianum strigillati, tubo longiores vel breviores sed numquam aequilongiores. Stamina epipetala in tubo profundae didynama vel aequaliter longa. Antherae extrorsae longitudinaliter dehiscentes. Fructus capsulares aut baccatus. Embryo parum curvus. Plantae praecipue alcaloidam “Scopolamin” et steroid-saponinem continentis.

Woody shrubs inhabiting Australia. Corolla with rolled, inflexed-valvate aestivation of the 5 lobes, these striated along main veins, varying in length but never as long as the tube. Stamens didynamous or equal, epipetalous low in corolla tube, the anthers dehiscing extrorsely by longitudinal slits. Fruit capsular or baccate. Embryo only slightly curved. Plants containing predominantly the alkaloid scopolamine and steroid saponins. Type: *Anthocercis* Labill.

Subfamily ATROPOIDEAE Tétényi, subfam. nov.

Plantae ex orbe antiquo oriundae. Herbae locis calidis excepto occurrentes, aut plantae lignosae endemicae regionis montium excelsium vel insularum. Corolla tubulosa vel campanulata. Lobi corollae aestivatione imbricati. Stamina quinque aequalia. Fructus baccatus vel capsularis. Embryo circulariter vel spiraliter curvatus. Plantae praecipue alcaloidam “Hyoscyamin” et steroidalcaloidam continentis.

Herbaceous plants of the Old World, occurring exceptionally as endemic woody shrubs on mountains or islands in warmer regions. Corolla tubular or campanulate, the aestivation of lobes imbricate. Stamens 5, equal. Fruit baccate or capsular. Embryo curved circularly or in a spiral.

Plants containing predominantly the alkaloid hyoscyamine and steroidal alkaloids. Type: *Atropa* L.

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